The genus Plagiochasma and its North American species *

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(WITH EIGHT TEXT FIGURES)

HISTORICAL INTRODUCTION

Of the various Marchantiaceae occurring in North America the genus *Plagiochasma* has long been in especial need of critical study and revision. It is hoped that the present paper may clear up some of the confusion and misunderstanding regarding it, although the writer admits that further work will be necessary before our knowledge of the species can be considered at all complete. Prolonged observation in the field under varying conditions of light and moisture is especially to be recommended, while further collection of material, particularly in fruiting condition, is much to be desired. Fortunately dried specimens are more satisfactory for study than in most genera of the thallose liverworts, even if they can never take the place of material properly fixed and preserved.

The genus *Plagiochasma* Lehm. & Lindenb., as originally proposed by its authors in 1832 (**17**, p. 13), contained two undescribed species from Nepal, *P. cordatum* and *P. appendiculatum*. The first of these should be regarded as the type of the genus. Four years later Lehmann (**16**) published another genus, *Anthrocephalus*, which was likewise based on an undescribed species from Nepal, *A. nepalensis*. In 1838 Nees von Esenbeck (**26**, pp. 33, 40) accepted both of these genera. He pointed out the fact, however, that *Aytonia rupestris* Forst. was referable to *Plagiochasma*, and he added a new species, *P. peruvianum* Nees & Mont., to this genus. *Aytonia rupestris*, which was published in 1776, was based on material collected by its authors on the island of Madeira, but Nees von Esenbeck was able to extend its known range to the island of Corfu, in Greece, citing specimens collected by Spathys. Even at the time he wrote the species had received many names, but he discarded them all and renamed the plant *P. Aitonia* Lindenb. & Nees.

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* Contribution from the Osborn Botanical Laboratory.

Between 1838 and 1846 Sassi (**27**) proposed *Anthrocephalus italicus* as a new species, his material having been collected near Finale in Liguria, and the following species of *Plagiochasma* were published: *P. Rousselianum* Mont. (**23**, p. 334, *pl. 9, f. 1*), of western Algeria; *P. chlorocarpum* (Nees & Mont.) Mont. (**24**, p. 59), of Chile; and *P. validum* Bisch. (**3**, p. 56, *pl. 56, f. 2753*), also of Chile. The number of species was thus increased to two in *Anthrocephalus* and to seven in *Plagiochasma*.

In 1846 the part of the Synopsis Hepaticarum which treated the Marchantieae appeared (**11**, pp. 511–521) and the authors of this important work showed that the genus *Anthrocephalus* was based on poorly developed specimens of a *Plagiochasma*, which they renamed *P. Colsmannianum* Lehm. & Gottsche, thus discarding Lehmann's specific name *nepalensis* altogether. For some reason they make no mention of *A. italicus*, possibly because Sassi's work was unknown to them. In addition to *P. Colsmannianum* and the seven species of *Plagiochasma* already known they include the following species in the genus: *P. intermedium* Lindenb. & Gottsche, of Mexico; *P. australe* (Tayl.) Nees, of New Zealand; *P. limbatum* (Tayl.) Nees, of Ascension Island; *P. elongatum* Lindenb. & Gottsche, of Mexico; and *P. mexicanum* Lindenb. & Gottsche, also of Mexico. They thus increased the total number of species to thirteen.

In 1849 a posthumous work of Griffith was published in which four news species of *Plagiochasma* from India were described (**12**, pp. 330, 331, 337, *pl. 65, 68, 69e*), namely: *P. paradoxum* Griff., *P. pedicellatum* Griff., *Anthrocephalus polycarpon* Griff., and *A. megacarpon* Griff. In 1856 Sullivant (**38**, p. 688, *pl. 6*) published *P. Wrightii*, a new species from Texas. In 1859 DeNotaris (**5**, p. 476, *pl. 1*) showed that *Anthrocephalus italicus* was clearly a species of *Plagiochasma* and transferred it to the latter genus under the name *P. italicum*. In 1863 Gottsche (**10**, p. 266) described a new species of *Plagiochasma*, *P. crenulatum*, from Mexico. In 1869 Austin (**1**, p. 229) described, as a new species, *P. erythrospermum* Sulliv., from the Rocky Mountains.

In 1868 Lindberg (**20**, p. 291) revived the generic name *Aytonia* of Forster and secured a number of followers in both Europe and America. He spelled the name "*Aitonia*," which was perhaps justifiable, both spellings having been used by the original authors. In 1874, Dumortier (**7**, p. 148) discarded both *Plagiochasma* and *Aytonia* and applied the name *Otiona* of Corda to the genus. In 1877 Trevisan (**39**, p. 436) revived the name *Rupinia* of the younger Linnaeus. In 1894 Le Jolis (**19**, pp. 109–116) gave excellent reasons for discarding the names *Aytonia*, *Otiona*, and *Rupinia*, and for retaining the name *Plagiochasma*. This course is now advocated by both Stephani and Schiffner, who included *Plagiochasma* in their proposed lists of *nomina conservanda* presented at the International Botanical Congress of Brussels in 1910. The name *Plagiochasma* is therefore used in the present paper.

In 1881 Leitgeb (**18**, p. 51) showed that *P. Rousselianum* belonged in the genus *Clevea*, proposed by Lindberg in 1868, and the species is now known as *C. Rousseliana* (Mont.) Leitg. In 1899 Howe (**14**, p. 39) showed that *P. erythrospermum* was a synonym of *Clevea hyalina* (Sommerf.) Lindb. Between 1881 and 1898 the following species of *Plagiochasma* were published (some of them under the name *Aitonia*): *A. subplana* Spruce and *A. lanigera* Spruce (**32**, pp. 567, 568), both of Ecuador; *A. extensa* Steph., of Australia (**33**, p. 17); *A. eximia* Schiffn., *A. Fischeriana* Steph., and *A. microcephala* Steph. (**34**, pp. 300, 301) all three of Africa; *A. fissisquama* Steph. of China (**35**, p. 209); *A. japonica* Steph., of Japan (**36**, p. 54); and *P. pterospermum* Massal., of China (**21**, p. 46, *pl. 13, f. 18*). The various species added to the genus since the Synopsis Hepaticarum increased the total number to twenty-eight.

In 1898 Stephani (**37**) published the last general account of *Plagiochasma* in his Species Hepaticarum. With the exception of Griffith's species, three of which he mentions but does not describe on account of the lack of available material for study, he recognizes as valid all the species previously published. He intimates, however, that *P. pterospermum* is probably a synonym of *P. fissisquamum*. Besides transferring to *Plagiochasma* the various species described under *Aitonia* he restores to *P. Aitonia* and *P. Colsmannianum* their original specific names and describes them as *P. rupestre* and *P. nepalense* respectively. He likewise proposes the following seven species as new: *P. dschallanum*, *P. tenue*, *P.*

algericum, *P. Beccarianum*, and *P. Schimperi*, all from Africa; *P. coerulescens* Nadeaud, from Tahiti; and *P. brasiliense*, from Brazil. Since 1898 the following new species of *Plagiochasma* (or *Aytonia*) have been published: *Aytonia Evansii* Haynes and *A. jamaicensis* Haynes, both from Jamaica (**13**); *P. abyssinicum* Gola, from Abyssinia (**9**, p. 62); and *P. articulatum* Kashyap, from India (**15**, p. 320, *f. 8*). It should be noted further that *P. italicum* was reduced to a synonym of *P. rupestre* by K. Müller in 1907 and that this reduction was sanctioned by Schiffner (**25**, pp. 252, 254). In the review of the literature just given no allusion is made to papers which simply record extensions of range of individual species.

If, now, the four species of Griffith are ignored and the reduction of *P. italicum* to synonymy is accepted, the seven species added by Stephani in 1898 and the four subsequently published increase the total number of species of *Plagiochasma* to thirty-four. Of these species *P. rupestre* has been recorded from various stations in Europe, Asia, and Africa, and *P. elongatum* from both North America and Asia, while the others are distributed as follows: Asia, seven species; Africa, ten; North America, six; South America, six; Australia and the islands of the Pacific, three.

The genus is most at home in arid portions of the tropics, many of the species growing on calcareous rocks. *P. rupestre*, however, extends as far north as the Mediterranean portions of Europe and *P. australe* (as already noted) was based on New Zealand material. On account of the dry habitats the sperms often fail to reach the archegonia, and even where fertilization takes place the normal development of carpocephala and sporophytes may be prevented by periods of drought. Immature and abnormal carpocephala due to such causes have produced much of the confusion in the interpretation of the genus and its various species.

MORPHOLOGY OF THE GENUS

Our knowledge of the morphology of *Plagiochasma* is largely based on the work of Leitgeb (**18**, pp. 63–68, *pl. 1*), although later writers have added important details. For a resumé of the work done on the genus the Inter-Relationships of the Bryophyta by Cavers may be consulted (**4**). Recent writers agree in placing

Plagiochasma in Leitgeb's group Operculatae (or its equivalent) of the Marchantiaceae. It represents the most simply organized member of the group, but there is a strong tendency at the present time to consider it reduced rather than primitive.

The species of *Plagiochasma* grow in depressed and intricate mats. The thallus is remarkably uniform in structure throughout the genus and shows clearly the usual differentiation into an epidermis, a photosynthetic layer with intercellular spaces, and a compact ventral layer, from the lower surface of which arise the ventral scales and the rhizoids. The thallus is sometimes continuous in its growth, maintaining the same width, and sometimes seems to be divided into a succession of joints, each joint springing from the apex of an older joint and rapidly increasing in width. According to Leitgeb this condition is not due to apical innovations but simply to the fact that the growth of the thallus is subject to interruptions, the new portions being narrower when the growth is first resumed. According to Kashyap, however, true apical innovations occur in *P. articulatum*. In addition to the usual branching by dichotomy, in which both branches are alike, the thallus often bears ventral adventive branches, which broaden out rapidly from a stalk-like base. The authors of the Synopsis Hepaticarum (**11**, pp. 511–521) supposed that these branches were never produced by species in which the thallus was jointed and they therefore divided the genus into two sections, as follows: § 1. Frons ex apice cordato articulatim innovans; § 2. Frons e ventre innovans, apice saepe subcontinua. Leitgeb showed, however, that *P. intermedium* of § 1 often developed ventral branches, that *P. appendiculatum* of § 2 often appeared jointed, and that the distinction relied upon in the Synopsis was therefore inconstant and to be used with caution.

The epidermis, as in most genera of the Marchantiaceae, consists of a single layer of pale or colorless cells, although the cell-walls are sometimes more or less pigmented with purple. The walls are usually firm but thin and this is true even of the cuticle. The latter, however, sometimes appears thickened, roughened, and slightly opaque, owing to the deposition of a waxy substance on the surface. When this is present the thallus is bluish or glaucous green instead of bright green. Trigones can always be demonstrated in the epidermis and are often large and conspicuous, but in certain species their size is very variable and depends on external conditions.

The epidermal pores of the thallus as noted by Leitgeb, are of two distinct types. In the first (FIG. 1) the opening is small and often difficult to demonstrate, especially when more or less stopped up by the waxy secretion on the cuticle. Around this small opening there are usually from four to six bounding cells, the radial walls between which are normally more or less thickened. Sometimes one or more of the bounding cells will be divided by a

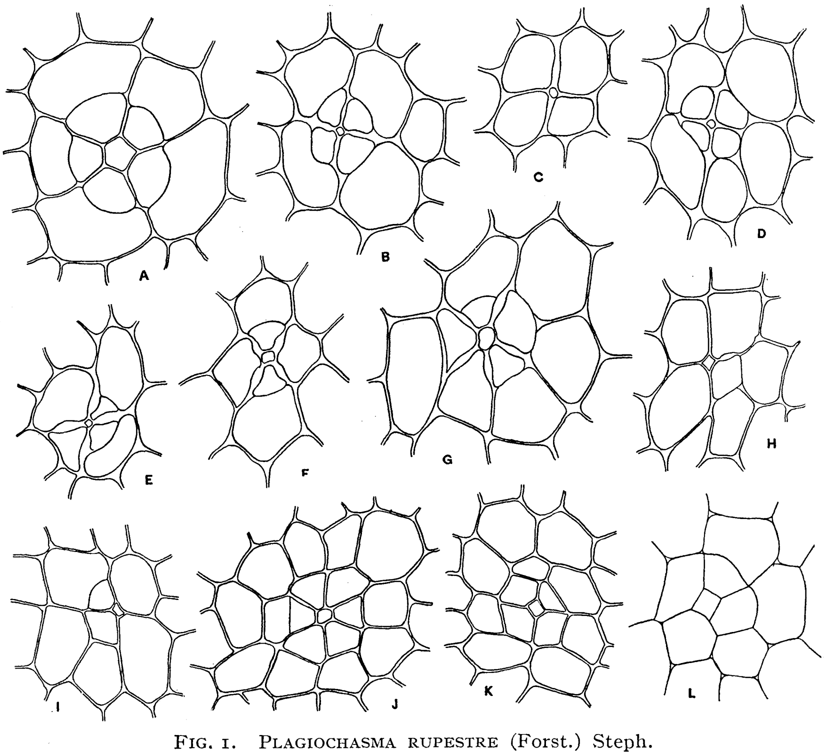

FIG. 1. PLAGIOCHASMA RUPESTRE (Forst.) Steph.

A series of epidermal pores from various specimens, × 300. A. Italy, *D. Lanza*, in V. Schiffner's Hep. Europ. Exsic. No. 10. B, C. Canary Islands, *C. J. Pitard*, in Plant. Canar. No. 762. D. Baja California, *T. S. Brandegee*. E. Puebla, *F. Liebmann*, type of *P. mexicanum*. F. Jalisco, *Barnes & Land 123*. G. Morelos, *Barnes & Land 480*. H. Oaxaca, *F. Liebmann*, type of *P. elongatum*. I. Jalisco, *Barnes & Land 134*. J–L. Arizona, *G. E. Nichols*, the last figure drawn from material cultivated in the laboratory.

periclinal wall (with respect to the pore), and the opening under such circumstances may be described as surrounded by two more or less complete concentric series of cells. The cells surrounding the openings are not elevated and are usually much like the other epidermal cells. When the radial walls between them are slightly or not at all thickened, as is sometimes the case in certain species, the entire pore-structure is very inconspicuous.

In pores of the second type (FIGS. 5–8, A), although the opening itself is not necessarily larger than in pores of the first type, the whole structure is much more evident because it is more or less raised above the general level of the epidermis and because the cells surrounding the opening are in two or more concentric series with six to eight or even more cells in each series. It is convenient to describe these cells, which differ considerably in form from the other epidermal cells, as being arranged in radiating series with two or more cells in each series. In many cases the walls separating these are distinctly thickened. Immediately bounding the opening a circular ridge is present which appears to be formed by the thickened and coalescent inner walls of the surrounding cells. Deutsch (**6**, p. 494, *f. 9*), however, has recently shown that in the very similar pores of *Targionia hypophylla* L. the ridge consists of a circular row of dead and collapsed cells with thickened and highly cutinized walls. Apparently his explanation would apply equally well to the pores of the second type in *Plagiochasma*, and it is sometimes possible to demonstrate the radial walls between the collapsed cells. The presence of this circular ridge in the second type of pore and its absence from the first type is perhaps the most important difference between them.

It will be noted when the pores of *Plagiochasma* are compared with those of other genera of the Marchantiaceae that those of the first type are essentially like the pores found in *Oxymitra* and in the various genera of the Astroporae, while those of the second type find their counterparts in the other genera of the Operculatae, as well as in certain genera of other groups. Both types stand in marked contrast to the complex pores of *Marchantia*, *Preissia*, and *Bucegia*, where the cells surrounding the opening are in several layers. Even in *Plagiochasma*, however, complex pores of the marchantiaceous type are present on the carpocephala.

The photosynthetic tissue contains several layers of intercellular spaces, separated from one another by plates of green cells a single cell in thickness. These spaces, which vary greatly in size in different species, are connected with one another by means of holes through the green partitions, and some of them communicate directly with the outside air by means of the epidermal pores. According to Leitgeb (**18**, p. 64) the thallus first forms primary intercellular spaces or air chambers, each of which has its pore, and these chambers afterwards become divided up by secondary plates of cells which grow out from the primary partitions. Barnes and Land (**2**, pp. 210–213, *f. 17–22*) admit that such a partitioning of chambers in *Plagiochasma* may perhaps occur to a limited extent, but they show clearly that some of the air-spaces without epidermal pores are formed directly, in very young segments, by the splitting apart of cells originally united.

The compact ventral tissue is not highly developed. In the median portion of the thallus it attains a thickness of perhaps ten to twenty cells, but it thins out rapidly on each side until it becomes only one cell thick and forms the ventral walls of the air-chambers. It is composed of thin-walled cells, a few of which contain oil-bodies, but it shows no signs of the slime cavities or the fibrous cells which occur in some of the more complicated Marchantiaceae. Sometimes, but not always, mycorrhiza is present in the ventral tissue, occupying cells in the median portion just below the green tissue. The cells containing the mycorrhiza sometimes have their walls pigmented with purple, but this is not invariably the case.

The rhizoids are of the two types usually found in the Marchantiales and require no especial comment. The ventral scales, however, which are in two regular rows, are unusually well developed and exhibit considerable variety in form and structure, sometimes even in a single species (see FIGS. 2, 3). They show the characteristic division into basal portion and appendage or appendages. The basal portion is ovate to lunulate in outline and is attached by an oblique line extending forward from the median region half way to the margin or beyond. In the apical part it narrows gradually or abruptly into the appendage or appendages, the number of these structures often varying from one to three on a single thallus. The appendages vary in form from narrowly lanceolate to orbicular, when the genus as a whole is taken into account, and they likewise vary markedly in size. As in other genera of the Marchantiaceae the appendages are the first part of the scale to develop, covering over the embryonic region at the growing point and being gradually pushed into a ventral position by the apical elongation of the thallus. The basal portion and the appendages are usually deeply pigmented with purple, but the color of the appendages in particular often becomes bleached

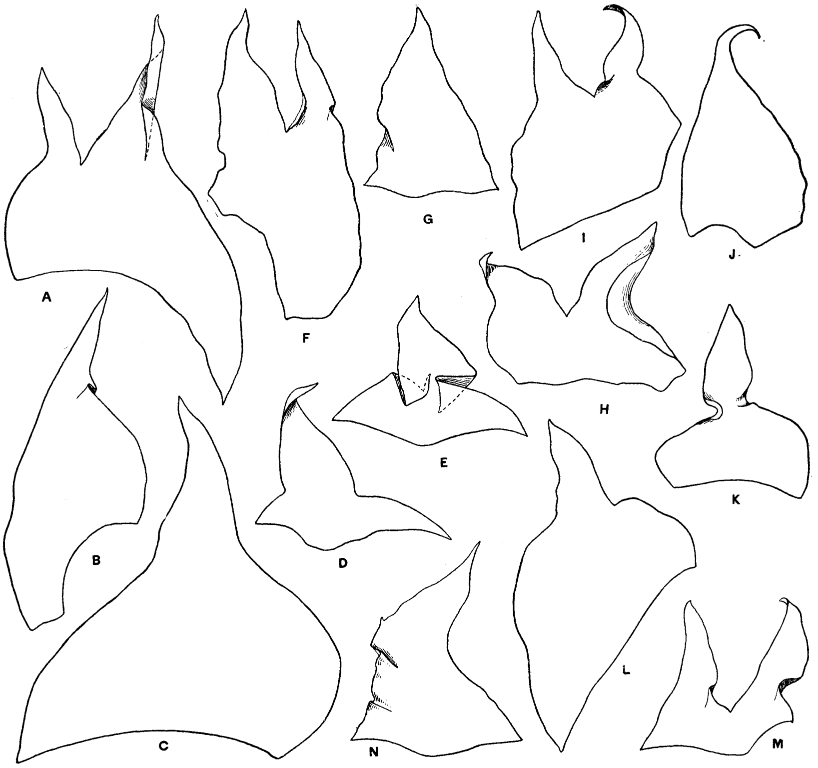

FIG. 2. PLAGIOCHASMA RUPESTRE (Forst.) Steph.

A series of ventral scales (or their appendages) from specimens collected in various parts of Europe and the Atlantic Islands. A, B. Italy, *D. Lanza*, in V. Schiffner's Hep. Europ. Exsic. No. 10. C, D. Madeira Islands, *W. Trelease*, × 40. E–G. Canary Islands, *O. Kuntze*, × 27. H. From the same specimen, × 17. I–L. Canary Islands, *C. J. Pitard*, in Plant. Canar. No. 762, × 40. M. Ascension Island, *J. D. Hooker 22*, type of *P. limbatum*, × 27. N. From the same specimen, × 40.

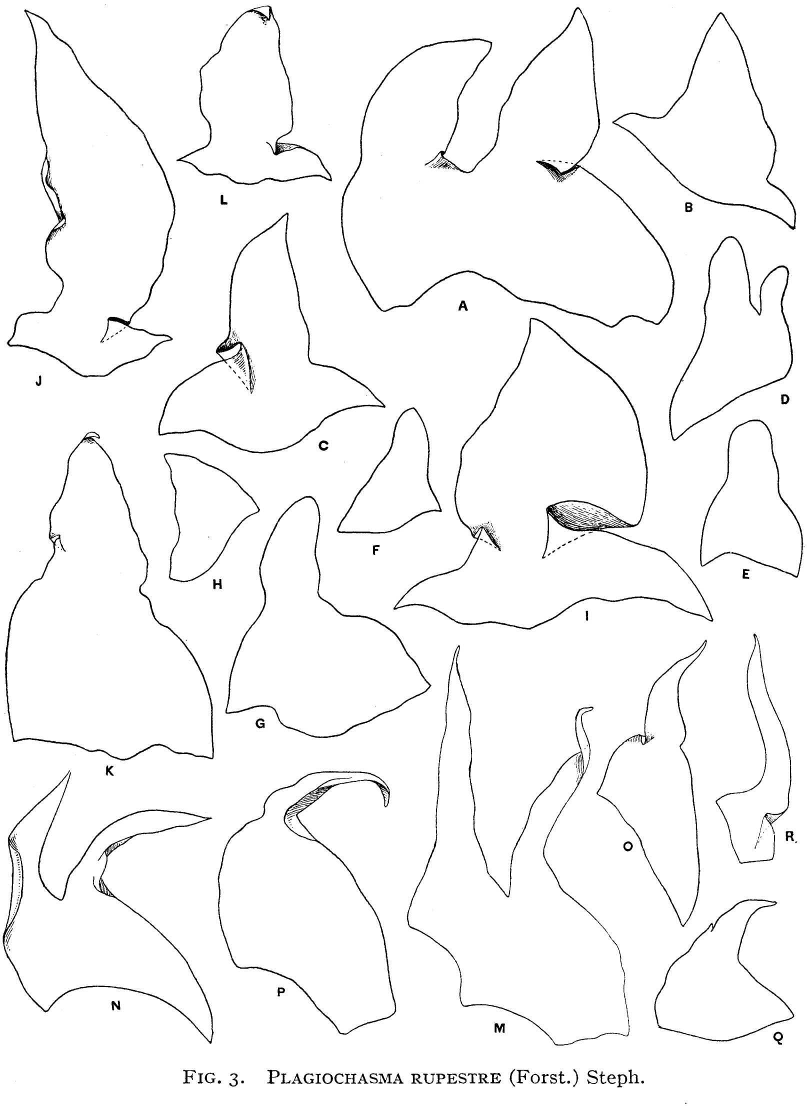

FIG. 3. PLAGIOCHASMA RUPESTRE (Forst.) Steph.

A series of ventral scales (or their appendages) from various North American specimens. A–F. Arizona, *G. E. Nichols*, × 40, the last three figures drawn from material cultivated in the laboratory. G, H. Arizona, *W. A. Cannon*, × 40. I, J. Baja California, *T. S. Brandegee*, × 40. K, L. Morelos, *C. G. Pringle 15319*, × 40. M–O. Jalisco, *Barnes & Land 123*, × 17. P. Morelos, *Barnes & Land 480*, × 40. Q. From the same specimen, × 17. R. Oaxaca, *F. Liebmann*, type of *P. elongatum*, × 40.

out with age. The scales are a single cell in thickness except near the base. The cell-structure is sometimes uniform throughout, but the marginal cells are sometimes irregular and project as indistinct teeth bearing slime papillae or their vestiges (FIG. 5, D). The cells containing oil-bodies, on account of their small size and lack of pigmentation, form a striking feature of the scales. They are sometimes confined to the basal portion and sometimes occur in the appendages as well.

With regard to the inflorescence certain species of *Plagiochasma* are described as dioicous and others as monoicous, while some are said to be either dioicous or monoicous. Unless the male and female plants grew in separate mats, a dioicous inflorescence would be difficult to demonstrate beyond doubt on account of the fact that the androecia are often borne on ventral branches, which easily become separated and present the appearance of being distinct plants. It is therefore probable that some of the so-called dioicous species are really monoicous. Stephani (**37**, p. 777) mentions an interesting case which shows how variable the inflorescence can be and how easily a hasty observation could lead to error. In the thallus he described he found five joints, the first, second, and fourth of which were male, the third and fifth female. Each joint bore ventral branches, the male joints in most cases bearing female branches and the female joints male branches. Among the ventral branches he found further certain ones which bore both male and female inflorescences in succession and others which forked, one fork being male and the other female. Schiffner (**28**, p. 15) has described material of *P. italicum* in which the inflorescence was equally variable. In both these cases the inflorescence might properly be described as heteroicous, and this term would probably apply to most monoicous species and to many which are supposed to be dioicous.

The antheridia, as in most of the other Marchantiaceae, are grouped in definite discoid inflorescences or androecia, slightly raised above the dorsal surface of the thallus and apparently not affecting its subsequent growth. The androecia vary in outline from circular to more or less crescentic or cordate, with the convex side turned toward the base of the thallus. These crescentic androecia, as Leitgeb notes, should not be confused with the dichotomous androecia occasionally found in *Lunularia*, where two growing points are involved (**18**, p. 26). They represent, according to his ideas, a persistence of the two-lobed condition at the apex of an ordinary thallus, where the single growing point lies in the indentation between the lobes. Kashyap (**15**, pp. 318, 321), however, says that in both *P. appendiculatum* and *P. articulatum* the androecium usually has two growing points and implies that the horseshoe shape is therefore due to a forking. Unfortunately, he presents no conclusive evidence to support his position. The antheridia are of the usual marchantiaceous type. Each one lies at the bottom of a deep depression, the roof of which forms a distinct bluntly conical ostiole with a minute opening at the tip. Between the ostioles the epidermis of the androecium shows numerous pores and these, as recently demonstrated by Kashyap, are of the same type as in the vegetative thallus. In cases where the normal pores are complex and show many radiating series of cells with several cells in each series, the androecial pores tend to be more simple and to show fewer series of cells and fewer cells in each series. A row of delicate and slender scales, usually pigmented with purple, surrounds the androecium.

The carpocephala arise singly or in short median rows from the dorsal surface of the thallus and apparently in most cases neither stop nor interrupt its further elongation. Each carpocephalu mcommonly bears three or four archegonia evenly distributed around its margin (Leitgeb, **18**, p. 29) although in *P. appendiculatum*, according to Kashyap, the number is frequently five or six and may be as high as nine. Through the extensive growth of the upper median portion and of the parts adjacent to the archegonia, the latter are displaced to the lower part of the carpocephalum and each one eventually lies at the bottom of a groove which is bounded by two folds of tissue. In case fertilization has taken place the grooves become much deeper through the continued growth of the folds, the edges of which come together and grow inwards toward the developing sporophyte, as originally described and figured by De Notaris in the case of *P. rupestre* (**5**, p. 480, *pl. 1*, *f. 20–26*); where the folds meet at their upper ends they form a more or less distinct apiculum or horn. No pseudoperianths of any sort are developed. Around the margin of the carpocephalum a circle of slender scales (see FIGS. 4, E; 5, E–G; etc.) makes its appearance very early; these scales, according to Leitgeb (**18**, p. 67), are in two series and they show the same purple pigmentation as the androecial scales, becoming bleached out with age. When the capsules have reached maturity the region between the carpocephalum and the thallus undergoes intercalary growth and elongates into a stalk, some of the scales remaining at the base and some being carried up with the carpocephalum. The length of the stalk varies greatly in different species and even in the same species under different conditions. Sometimes it is so short that it scarcely raises the carpocephalum above the thallus. The stalk is remarkable on account of the fact that it possesses no rhizoid-furrow, although it may be irregularly grooved.

With regard to the morphology of the carpocephalum in *Plagiochasma* and in *Clevea*, where similar conditions obtain, the opinions of writers vary. Leitgeb (**18**, p. 29) considered the whole structure a highly developed dorsal outgrowth of the thallus, comparable with the low outgrowths found in *Corsinia*. He based his conception on the continued growth of the thallus after the initiation of the carpocephalum and on the lack of a rhizoid-furrow in the stalk, both indicating that the growing point of the thallus was not involved. He therefore considered that the carpocephalum in these two genera was morphologically different from the very similar carpocephalum found in *Reboulia*, *Sauteria*, and more complex forms, where the initiation of the carpocephalum brought the growth of the thallus to an end and where the stalk showed one or two rhizoid-furrows. In these cases he considered that the carpocephalum represented a modified shoot (or shoot-system) in which the growing point of the thallus was directly involved. Leitgeb's views regarding the androecium were very similar. Not only in *Plagiochasma* but also in *Reboulia* and other genera, where the development of the androecium failed to stop the growth of the thallus, he considered the structure a mere dorsal outgrowth and therefore morphologically different from the androecium in *Preissia* and related genera, where it represented a modified shoot.

Goebel (**8**, p. 46) has recently pointed out that these ideas involve certain difficulties. He emphasizes the improbability of having the male and female inflorescences morphologically different in a single genus, such as *Reboulia*, or in a group of related genera, and he brings out the fact that if the carpocephalum of *Plagiochasma* is really a dorsal outgrowth, as Leitgeb claimed, then its scales would have to have a different significance from the very similar scales found on a carpocephalum which represents a branch system. In the latter case the scales are modified ventral scales, homologous with those found on an ordinary thallus. In *Plagiochasma*, however, the scales if considered homologous with the ventral scales would imply an inversion of the dorsi-ventrality of the thallus to account for their dorsal position; if considered morphologically different from the ventral scales, they would have to be regarded as developed from structures normally present on the dorsal surface, such as the hairs found in certain species of *Riccia*, or the slime-papillae which occur in the cupules of *Marchantia*. Neither of these interpretations seems plausible.

Goebel shows further (**8**, pp. 85–88) that these difficulties of interpretation are avoided if such genera as *Reboulia* and *Plagiochasma* are considered as reduced from the more complex *Marchantiaceae* rather than as primitive forms from which the more complex genera have been evolved. In *Marchantia*, for example, where the complexity perhaps reaches its highest expression, both the androecium and the carpocephalum represent stalked branch-systems, the sexual organs arising in acropetal succession on the evident branches. A first indication of reduction appears when the branches lose their distinctness although the acropetal succession of the sexual organs remains apparent. This is seen in the androecium of *Preissia*. A second indication is a reduced development of the stalk, leading to its final disappearance, as seen in the androecia of *Conocephalum* and its allies. A third step in the reduction, according to Goebel's account, is a change in the position of the inflorescence, which is perhaps caused by a very early appearance of an apical innovation. This may occur even in inflorescences which retain their stalks. In many cases such an innovation is not started until the inflorescence is already established, when it shows its character clearly as a new shoot broadening out from a narrow base. Such a condition is evident in the carpocephalum of *Reboulia* and also in the curious *Plagiochasma articulatum*, according to Kashyap's account (**15**, p. 320). If, however, the innovation starts much earlier it might seem to continue the growth of the thallus without an interruption and thus to displace the inflorescence to an apparently dorsal position. The latter would still represent a modified shoot, the scales would still be homologous with ventral scales, and a thallus which showed a median dorsal row of such inflorescences would really be a sympodium. The change in position just described is clearly seen in the androecium of *Reboulia* and in both the male and female inflorescences of most species of *Plagiochasma*. In the case of the androecium of *Bucegia*, recently investigated by Schiffner (**30**), all gradations in the process have been demonstrated.

It is perhaps not necessary to assume that the carpocephalum in *Plagiochasma* actually involves the growing point of the thallus and that a new growing point must be differentiated before the growth can be continued. If the important part played by intercalary growth in the development of the carpocephalum is taken into account such an assumption becomes superfluous. Even in such complex carpocephala as those of *Marchantia* the growth of the stalk and of the upper part leading to the displacement of the archegonia to the lower surface is intercalary in character. In *Reboulia*, after the earliest rudiment of the carpocephalum is laid down in the young segments derived from the growing point, the later development is entirely intercalary, as Leitgeb himself admits (**18**, p. 31), and the growing point, carried upward by the elongating stalk, plays no part whatever in the process. In *Plagiochasma* the first beginning of the carpocephalum is developed from young segments just as in *Reboulia*, and from this rudiment the mature structure develops by intercalary growth in the same way. The mere fact that the growing point is not carried upward by the elongating stalk but continues directly the growth of the thallus does not invalidate the homology of this carpocephalum with that of *Reboulia*. In both cases the structure owes its initial stages to the activity of the growing point of the thallus and its later stages to intercalary growth, and in neither case does the growing point play any active part in these later stages. Of course what is here said about the carpocephalum would apply in most respects to the androecium as well.

In case the growing point of the thallus is not used up in the development of the inflorescence the latter becomes a lateral or dorsal branch, and the shoot which bears a series of such inflorescences would be a monopodium and not a sympodium. Such a change from a sympodium to a monopodium would not be unique. Goebel (**8**, p. 91) quotes similar examples from the inflorescences of the Boraginaceae and from the vegetative shoots of the Vitaceae. And the further reduction from such a monopodium through *Corsinia* to *Riccia*, where the sexual organs are not in distinct inflorescences and where the intercalary growth so prominent in the carpocephala of *Reboulia* and *Plagiochasma* has become largely or wholly eliminated, would be easily intelligible.

In classifying the species of *Plagiochasma* Stephani (**37**) lays a great deal of stress upon the shape of the carpocephalum. He divides the genus into two groups, "*a*" and "*b*." In "*a*" the carpocephalum is said to be more or less convex; in "*b*," more or less excavated at the vertex. From the writer's observations this distinction is not constant. In at least one species which Stephani places in division "*a*," namely *P. japonicum*, the carpocephala examined were distinctly concave, and even if this condition should be proved exceptional its occasional presence would invalidate Stephani's classification. It is quite possible that the form of the carpocephalum is influenced by external condition, although no experimental evidence can be brought forward to support this idea.

The sporophyte of *Plagiochasma* is described in its essential features by Leitgeb (**18**, p. 67). He calls attention to its well-developed foot and scarcely evident stalk and to the fact that the wall of the capsule consists of a single layer of cells except in the apical portion, which shows a circular region three cells thick. This he regards as a rudimentary lid although it does not separate at maturity as a typical lid would do. The capsule, in fact, dehisces irregularly and leaves behind a shallow urn with indefinite teeth or lobes around the rim. The cells of the capsule wall are destitute of the annular or half-annular thickenings found in so many of the Hepaticae. Some of them show more or less distinct trigones, but many of them are thin-walled throughout. The very rudimentary lid was apparently considered by Leitgeb a sufficient reason for placing *Plagiochasma* among his Operculatae. Solms-Laubach (29, p. 12) has shown, however, that in Leitgeb's group Astroporae an equally definite lid is developed but that it is easily overlooked on account of the thickenings in the cells of the capsule wall. In spite of this fact the lack of annular thickenings in the capsule wall and the structure of the photosynthetic layer of the thallus would seem sufficient to exclude *Plagiochasma* from the Astroporae and to place it in the same group as *Reboulia*, *Grimaldia*, and *Neesiella*, whatever this group may be called.

Stephani (37, p. 776) describes the spores as large, yellowish, tetrahedral, and loosely reticulate on the convex face with high and rough lamellae. The tetrahedral form is of course due to the original arrangement of the spores in the tetrad resulting from the division of the spore mother cell. One face of each spore, the spherical or convex face, represents a fourth of the original surface of the tetrad (see FIGS. 4, F; 5, H; 7, H; 8, G). The other three faces, the plane faces, represent the regions of contact with the three other spores of the tetrad (see FIGS. 4, G; 8, H). Throughout the genus a broad border is formed where the three plane faces meet the spherical face, and three narrow ridges are developed along the edges of the pyramid formed by the three plane faces. In order to gain a clear idea of the reticulum described by Stephani it is advisable to pass in review a large series of spores and to select for study those which show the spherical face plainly and those in which the apex of the pyramid is turned toward the eye of the spectator. If this is done the meshes of the reticulum will be observed in their most diagrammatic position, and it will be seen that the reticulum extends over both spherical and plane faces. A regular reticulum has been observed by the writer in all the the species examined. Sometimes, however, in some or all of the spores in a capsule, the reticulum will be incomplete owing to the partial development of the bounding ridges. Since this condition occurs in species where a normal reticulum is usually developed it can not be used as a distinguishing peculiarity. The spores of *Plagiochasma*, in fact, in contrast to many genera of the Hepaticae, yield no very helpful differential characters in separating species.

The elaters in the majority of cases are like those found in other

Hepaticae and consist of long tapering cells with thin walls strengthened by from two to four spiral bands of thickening. Two interesting modifications, however, should be noted. In the first, the spiral bands, which are entirely free from one another in most elaters, are coalescent by means of one or more longitudinal bands (FIG. 5, I). In the second, no spirals at all are present but the wall of the elater is uniformly thickened and the cavity reduced to a narrow median canal (FIG. 8, I). Coalescence of the type found in the first modification seems to be unusual. It was first detected by Miyake (**22**, p. 223, *pl. 3, f. 3*) in the remarkable *Makinoa crispata* (Steph.) Miyake, of Japan, but it has since been observed by Schiffner (**29**, p. 24) in *Neesiella rupestris* (Nees) Schiffn., a widely distributed species of Europe and North America, and probably occurs in other genera. The second modification is apparently confined to the genus *Plagiochasma.* It was first noted by Gottsche in *P. intermedium* (**10**, p. 264) and is mentioned by Stephani as one of the characteristic features of *P. japonicum* (**36**, p. 84). Its occurrence has likewise been recorded by Kashyap (**15**, p. 320) in the case of *P. appendiculatum* and *P. articulatum*, and the writer has observed it in *P. eximium.* Although the uniform thickening of the elater-wall has been considered a good specific character, it is not a constant feature and must be used with caution. Even in *P. intermedium*, where it is certainly the usual condition, Leitgeb (**18**, p. 68) failed to find it in the material which he examined. In the case of *P. japonicum* Massalongo (**21**, p. 48, *pl. 13, f. 19*) has described and figured a var. *chinense*, based on Chinese specimens collected by Father Giraldi, in which some of the elaters showed rudimentary spiral bands, although most were of the more solid type. Miss Haynes, also, in a series of unpublished drawings based on Japanese material of the same species, collected by T. Yoshinaga, has represented elaters in which poorly developed and irregular bands were present. In *P. eximium* some of the elaters show spiral bands and others uniform thickenings and there are various gradations between them. In *P. appendiculatum* the solid type is said to be less common than in *P. articulatum*, and Kashyap associates it with exposure to dryness during the development of the capsule. In spite of these variations there are certain species in which a uniform thickening has never been observed, so that it is allowable to associate this peculiarity with certain species, even if they may sometimes develop elaters of the usual type.

DESCRIPTION OF THE NORTH AMERICAN SPECIES

The seven North American species with their known ranges, according to published records, are the following: *P. crenulatum*, Mexico; *P. elongatum*, Mexico and China; *Aytonia Evansii*, Jamaica; *P. intermedium*, Mexico and Guatemala; *Aytonia jamaicensis*, Jamaica; *P. mexicanum*, Mexico; and *P. Wrightii*, Texas. In the writer's opinion, however, *P. elongatum*, *Aytonia Evansii*, and *P. mexicanum* represent synonyms of the widely distributed *P. rupestre*. This reduction to synonymy would diminish the total number of North American species to five, if it were not for a Mexican species proposed as new, which raises the number to six. In certain cases it has proved possible to extend the known ranges of individual species to a considerable extent. The six species recognized in the present paper may be distinguished as follows:

Key to the North American species

Epidermal pores of the first type (see p. 264), inconspicuous, not elevated, usually surrounded by from four to six cells.	1. *P. rupestre* (p. 277).
Epidermal pores of the second type (see p. 265), conspicuous, elevated, usually surrounded by six or more cells.	
Elaters with spiral bands of thickening.	
Appendages of ventral scales almost as long as the scales, ovate to orbicular, abruptly acute or apiculate.	2. *P. crenulatum* (p. 288).
Appendages of ventral scales much shorter than the scales, ovate, apiculate.	3. *P. jamaicense* (p. 292).
Appendages of ventral scales lanceolate to ovate, acute or obtuse.	4. *P. Wrightii* (p. 294).
Appendages of ventral scales subulate, acuminate.	5. *P. Landii* (p. 298).
Elaters usually with uniformly thickened walls showing no signs of spiral bands of thickening.	6. *P. intermedium* (p. 301).

1. PLAGIOCHASMA RUPESTRE (Forst.) Steph.

Aytonia rupestris Forst. Char. Gen. Plant. 147. *pl. 74.* 1776.

Rupinia lichenoides Linn. f. Suppl. Plant. Syst. Veg. Ed. 13, 69. 1781.

Rupinia rupestris Swartz, Meth. Musc. 39. 1781.

Reboulia maderensis Raddi, Gior. Sci. Lett. Arti. 1821.

Corsinia lamellosa Nees & Bisch. Flora **13**: 401. 1830.

Sedgwickia hemisphaerica Bisch. Nova Acta Acad. Caes.-Leop. Carol. **17**: 1079. *pl. 70, f. 4.* 1835. Not Bowdich.

Plagiochasma Aitonia Lindenb. & Nees; Nees von Esenbeck, Naturg. Europ. Leberm. **4**: 41. 1838.

Anthrocephalus italicus Sassi, Atti Prim. Riun. Sci. Pisa 160. 1840.

Jungermannia (Fegatella) australis Tayl.; Hook. f. & Tayl. Jour. Bot. **3**: 572. 1844.

Jungermannia (Fegatella) limbata Tayl.; Hook. f. & Tayl. *l. c.* **4**: 95. 1845.

Plagiochasma australe Nees; G. L. & N. Syn. Hep. 515. 1846.

Plagiochasma limbatum Nees; G. L. & N. *l. c.* 516. 1846.

Plagiochasma elongatum Lindenb. & Gottsche; G. L. & N. *l. c.* 519. 1846.

Plagiochasma mexicanum Lindenb. & Gottsche; G. L. & N. *l. c.* 519. 1846.

Plagiochasma italicum De Not. Mem. Real. Accad. Sci. Torino II. **18**: 476. *pl. 1.* 1859.

Aitonia italica Lindb. Not. F. et Fl. Fenn. **9**: 291 (footnote). 1868.

Otionia rupestris Dumort. Hep. Europ. 148. 1874.

Otionia italica Dumort. *l. c.* 149. 1874.

Rupinia italica Trevis. Rend. Ist. Lomb. II. **7**: 785. 1874.

Rupinia rupestris Trevis. Mem. R. Ist. Lomb. III. **4**: 437. 1877.

Rupinia mexicana Trevis. *l. c.* 437. 1877.

Rupinia elongata Trevis. *l. c.* 437. 1877.

Rupinia limbata Trevis. *l. c.* 437. 1877.

Rupinia australis Trevis. *l. c.* 437. 1877.

Aitonia lanigera Spruce, Trans. Bot. Soc. Edinburgh **15**: 568. 1885.

Aitonia australis Steph. Hedwigia **28**: 129. 1889.

Aytonia elongata Underw. Bot. Gaz. **20**: 66. 1895.

Aytonia mexicana Underw. *l. c.* 66. 1895.

Plagiochasma rupestre Steph. Bull. Herb. Boissier **6**: 783. 1898.

Plagiochasma lanigerum Steph. *l. c.* 188. 1898.

Aytonia Evansii Haynes, Bull. Torrey Club. **34**: 57. *pl. 5.* 1907.

Thallus pale green and glaucous above with a narrow purple border, plane or somewhat canaliculate, strap-shaped, sometimes forking, sometimes innovating at the apex or with ventral branches, margin undulate, scarcely or not at all crispate, mostly 1–2 cm. long, and 5–7 mm. wide, thickness of thallus about one tenth the width; epidermis composed of thin-walled cells with small trigones and a thin minutely roughened cuticle with a waxy deposit, the cells mostly 18–30 μ in diameter; pores not elevated, small, surrounded by four to six cells in a single series or in an incomplete double series, radial walls usually distinctly thickened; aeriferous layer about one half the thickness of the thallus in the median portion, fairly compact with the air-spaces a little wider than the green cells, tending to extend at right angles to the epidermis; ventral scales deep purple, obliquely lunate to ovate, entire, with a few scattered cells containing oil-bodies, gradually narrowed into one or two (very rarely three) ovate-lanceolate to lanceolate or subulate appendages, acute to acuminate at the apex, slightly or not at all constricted at the base, entire: inflorescence monoicous: ♂ inflorescence on a small ventral branch or on an ordinary branch: ♀ receptacles borne singly or in a median longitudinal series; peduncle short, mostly 3 mm. long or less; carpocephalum concave at the apex, with two or three apiculate lobes, maturing two or three sporophytes; scales of carpocephalum abundant, narrowly subulate with elongated filiform points, entire: spores yellowish brown, 70–90 μ in diameter, minutely rugulose, reticulate, spherical face mostly with twelve to fifteen meshes, plane faces usually with three or four meshes, the meshes on both spherical and plane faces often incomplete; elaters mostly 250–400 μ in length and about 10 μ in diameter, with two to four spirals, sometimes more or less coalescent. [FIGS. 1–4.]

The following specimens have been examined:

NEW MEXICO: Organ Mountains, Filmore County, altitude 1800 m., July, 1897, *E. O. Wooton.*

ARIZONA: without definite locality or date, *H. H. Rusby;* Santa Catalina Mountains, April, 1913, *W. A. Cannon;* Soldier's Canyon, Santa Catalina Mountains, September, 1913, *G. E. Nichols.*

BAJA CALIFORNIA: without definite locality or date, *T. S. Brandegee 25.*

DURANGO: Tejamén, August, 1906, *E. Palmer 473, 474;* city of Durango and vicinity, 1896, *E. Palmer 709* (mixed with *Targionia hypophylla* L.).

JALISCO: wet banks and rocks, Barranca de Oblatos, Guadalajara, September, 1908, *Barnes & Land 122, 123, 134.*

MORELOS: San Antonio Falls, Cuernavaca, October, 1908, *Barnes & Land 480;* near Cuernavaca, July, 1908, *C. G. Pringle 15319.*

OAXACA: Comaltepec, Chuapam, *F. Liebmann* (type of *P. elongatum*); Barranca San Luis, April, 1906, *C. Conzatti 1619.*

PUEBLA: San Baltanzan, near Puebla, May, 1909, *J. Nicolas 2;* San Lorenzo Tehuacan, *F. Liebmann* (type of *P. mexicanum*).

SAN LUIS POTOSI: near San Luis, 1878, *Parry & Palmer 1016.*

ZACATECAS: near Conception del Oro, August, 1904, *E. Palmer 307.*

JAMAICA: on banks near Portland Gap, Blue Mountains, July, 1903, *A. W. Evans 213* (type of *Aytonia Evansii*); on banks and rocks near Content Gap, September, 1906, *A. W. Evans 613.*

BRAZIL: Rio Janeiro, April, 1875, *Glaziou 7402* (listed by Spruce as "*Fimbriaria* sp." in Rev. Bryol. **15**: 34. 1888); Rio Grande de Sul, August, 1905, *A. Bornmüller 4994* (distributed under a manuscript name of Stephani).

ECUADOR: near Baños, Andes, altitude 2,000 m., *R. Spruce* (distributed in Hepaticae Spruceanae as "*Aitonia lanigera*" and probably representing a part of the original material).

GALAPAGOS ISLANDS: Abingdon Island, September, 1906, *A. Stewart 8676;* Charles Island, October, 1906, *A. Stewart 940.*

PERU: Ollantaytambo, July, 1911, *H. W. Foote* (listed by the writer as "*P. chlorocarpum*" in Trans. Conn. Acad. **18**: 298. 1914).

BOLIVIA: near Mapiri, January, 1893, *M. Bang 1748* (listed by Rusby as "*Aitonia valida*" in Mem. Torrey Club **6**: 129. 1896); Pelichuco, altitude 3350 m., May, 1902, *R. S. Williams 2728;* lower Pelichuco Rio, altitude 900 m., April, 1902, *R. S. Williams 2738.*

ARGENTINA: Sierra de Ventana, January, 1892, *R. Hanthal 61.*

CHILE: Desert of Atacama, September–October, 1890, *T. Morong.*

ITALY: on walls near Voltri, Liguria, *J. Baglietto* (distributed in Rabenhorst's Hep. Europ. No. 85, as *P. italicum*); near Palermo, Sicily, *D. Lanza* (distributed from specimens cultivated at Prague, Austria, in Schiffner's Hep. Europ. Exsic. No. 10, as *P. italicum*).

MADEIRA ISLANDS: without definite localities or dates, *G.*

Raddi (type of *Reboulia maderensis*), *G. Don;* near Funchal, 1858, *Johnson;* Como do Lobos, August, 1896, *W. Trelease.*

CANARY ISLANDS: Palma, 1815, *C. Schmidt;* February, 1888, *O. Kuntze;* Bocco de Bufadero, Teneriffe, January, 1906, *C. J. Pitard* (distributed in Plantae canarienses, No. 762).

CAPE VERDE ISLANDS: Green Mountains, St. Vincent, date and collector unknown.

ASCENSION ISLAND: without definite locality or date, *J. D. Hooker 22* (type of *Jungermannia* [*Fegatella*] *limbata*).

ST. HELENA: without definite locality or date, *Lieut. Houghton 33.*

ABYSSINIA: locality, date, and collector unknown.

TRANSVAAL: Müller's Farm, *MacLea* (distributed in Rehmann's Hepaticae austro-africanae, No. 32, as "*Plagiochasma muricatum* Steph.," but probably representing a part of the type material of *P. tenue*).

AUSTRALIA: Swan River, West Australia, 1846, *T. Drummond.*

NEW ZEALAND: without definite locality or date, *J. D. Hooker* (type of *Jungermannia* [*Fegatella*] *australis*).

Aside from several other localities in Italy and the Atlantic Islands, *P. rupestre* has been recorded from Greece, from Dalmatia, from southern France and Corsica, from Portugal, from Cape Colony, and from Asia Minor. Whether the plant from Schen-si, China, collected by Father Giraldi in 1896 and described by Massalongo (**21**, p. 49) under the name *P. elongatum β ambiguum*, belongs here or not cannot be decided from lack of specimens. According to the description, which tells nothing about the epidermal pores, the spores are subrugose (or rugulose) and not reticulated. Such a peculiarity would exclude the plant not only from *P. rupestre* but probably from the genus *Plagiochasma* altogether. The author intimates, however, that the spores may not have been mature, so that no definite conclusions can be drawn from them.

Although *P. rupestre* has not been considered an especially variable member of the Marchantiaceae, it nevertheless exhibits considerable diversity in size, in color, in the distribution of its male and female inflorescences, and in the structure of certain of its organs and tissues. Some of this diversity at least is due to external conditions. The variations in size and in inflorescence have already been considered. With regard to color the thallus is sometimes green throughout but is usually more or less pigmented with purple. The pigmentation may be confined to the ventral scales, but it usually affects also the ventral surface from the scales to the edge and a narrow border on the dorsal surface; sometimes, in fact, the entire dorsal surface may be more or less colored, although this condition is rare.

The structure of the epidermis and its pores is also worthy of comment (FIG. 1). Not only do the epidermal cells vary markedly in size, but their walls differ in thickness and the trigones are sometimes conspicuous, with straight or convex sides, and sometimes hardly to be made out at all. The waxy layer on the cuticle, moreover, is sometimes so thick and opaque that it is difficult to see the epidermal cells beneath. The epidermal pores escaped the observation of the early authors, and even Nees von Esenbeck (**26**, p. 45) and DeNotaris (**5**, p. 477) said that no pores were present. Apparently Voigt, in 1879, was the first to detect them (**40**, p. 747, *pl. 9, f. 24, 25*). In *P. Aitonia* he says that the pores are the smallest known to him, that the cells bounding the opening differ from the other epidermal cells only in their thickened radial walls, that the inner angles of these cells are often cut off by walls thus forming two circles (of four cells each), and that the inner cells of these circles are often so small that they can easily be overlooked. In *P. italicum* he says that the pores are larger, that the radial walls are scarcely thickened, and that the inner cells of the two concentric circles are almost always distinct. His figure of the surface view, which is said to represent *P. Aitonia*, does not show the radial thickenings very clearly, but his account of the two species which he distinguishes brings out the amount of variation to be expected in *P. rupestre*. In the vast majority of cases the number of cells around the openings varies from four to six. In very rare cases three cells or more than six may be demonstrated. In the accompanying figures the great variations in the size of the opening, in the thickness of the radial walls, etc., are shown. Apparently the degree of thickness which the radial walls show varies with the size of the trigones in the neighboring epidermal cells. In cultivated material (FIG. 1, A, L) the cells tend to be large, the trigones to be small, and the radial thickenings to be very inconspicuous, but similar conditions are sometimes present in plants growing naturally, so that no very definite conclusions can be drawn with respect to the causes of such variation.

The older writers laid but little stress on the peculiarities of the ventral scales in distinguishing the species of the Marchantiaceae. Perhaps some of the recent writers have over-emphasized the importance of these characters, but in the genus *Plagiochasma* the scales are often very helpful in the determination of species. They are, however, subject to considerable variation, and this is seen especially well in the case of *P. rupestre*. In their most characteristic form the basal portion of the scale varies from

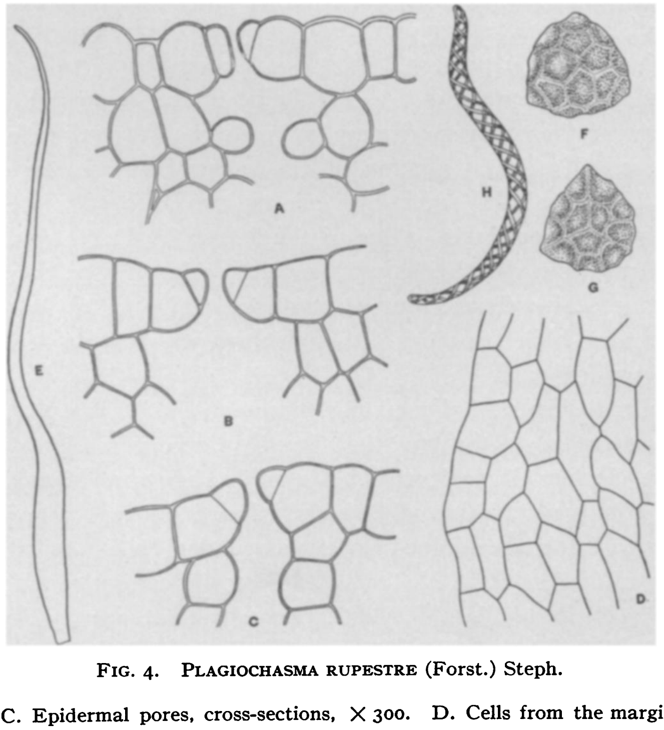

FIG. 4. PLAGIOCHASMA RUPESTRE (Forst.) Steph.

A–C. Epidermal pores, cross-sections, × 300. D. Cells from the margin of a ventral scale, basal portion, × 225. E. Scale from a carpocephalum, × 40. F. Spore, spherical face, × 225. G. Spore, plane faces, × 225. H. Elater, × 225. Figs. A and F–H were drawn from a specimen collected in Jalisco, *Barnes & Land 134;* Fig. B, from a specimen collected in Arizona, *G. E. Nichols;* and Figs. C–E, from a specimen collected in Morelos, *Barnes & Land 480.*

lunulate to ovate, while the appendages, one or two in number, are subulate and acute, without constriction at the base (see FIG. 2, A, B). Sometimes, when only one appendage is present there is no sharp boundary where it passes into the basal portion. The deviations from this characteristic condition are shown most clearly in the form of the appendages, which are sometimes ovate and more or less plicate at the base, and in their apices, which may be acuminate or, on the other hand, obtuse or even rounded, several of these variations being sometimes present on a single thallus or in a single clump (FIGS. 2, 3). The pigmentation of the scales is usually pronounced, although it may be absent in very moist environments and may disappear to a greater or less extent with age. The cells of the scales are fairly uniform throughout (see FIG. 4, D). Some of the marginal cells occasionally project as blunt or sharp denticulations, and in rare cases a distinct marginal tooth is present. It is much more usual, however, for the margin to be quite entire, and the peculiar slime papillae found in some of the other species are so evanescent that they leave no vestiges. The basal portion of the scale shows scattered cells with oil-bodies, and sometimes one or two such cells are to be seen in the appendages. One of the figures by DeNotaris shows a ventral view of a thallus with several scales in position. One of these scales shows four appendages. The writer has never observed so high a number, although three appendages were found in a very few cases.

In reducing *P. italicum* to a synonym of *P. rupestre* Müller calls attention to the fact that Stephani recognizes both species in his Species Hepaticarum. He adds, however, that he has sought in vain to find differential characters separating them, although he has examined specimens under both names in the Stephani herbarium. He found these to be almost exactly alike even in their details. The differences brought out by Stephani are the following: in *P. rupestre*, the dioicous inflorescence, the pore surrounded by five cells, the single narrowly lanceolate and acute appendage of the ventral scales: in *P. italicum*, the monoicous inflorescence, the pore surrounded by four cells, the one or two narrowly triangular appendages with broad bases. It will be seen at once that these differences are based on exceedingly variable characters, and it is not probable that many writers on the Hepaticae will dissent from Müller's reduction.

In the present paper several other species are considered synonyms of *P. rupestre*, and it might appear at first as if the reduction had been carried on in a somewhat wholesale way. In each case, however, the writer has based his opinion on the careful comparison of type specimens with authentic material of *P. rupestre* from Europe and the Atlantic Islands. It should perhaps be added that most of the species here reduced were proposed at a time when a plant was assumed to represent a new species if it came from a distant or isolated locality. The various species may be discussed in order.

In *P. australe,* which Stephani places just before *P. elongatum*, the following characters are emphasized: the monoicous inflorescence, the androecium being near the carpocephalum, the pore bounded by five cells, the lack of thickenings in the epidermal cells, the two appendages of the ventral scales, abruptly ligulate in outline, shortly acuminate, as long as the scales. In the portion of the type specimen examined some of these characters were not materialized. The cells of the epidermis, for example, although difficult to see on account of the thick and waxy cuticle, had distinct trigones, and the cells bounding the pores were four in number about as often as five. The radial walls, moreover, separating these cells were strongly thickened. With regard to the scales many of them showed a single appendage, and the form of this structure varied from lanceolate to ovate, the apex being acute. Of course these are only slight deviations from Stephani's account, which was based on Australian material collected by F. von Müller, and they are no more than would be expected in a variable species. Nothing was found in the type specimen which would warrant a separation from *P. rupestre*.

In the case of *P. limbatum*, which Stephani places in his section "*a*" (see p. 274), although he had not himself examined carpocephala, a portion of the original material, likewise in the Mitten herbarium, was examined. Here again nothing was found to warrant a separation from *P. rupestre*. The distinguishing characters, according to Stephani's account, are the following: the pronounced thickenings in the radial walls of the cells bounding the pores, the appendages of the ventral scales, often double, long-acuminate from a broad base, papulose on the margin. The papulose margin is unfortunately no more pronounced than it sometimes is in specimens of *P. rupestre* from other localities, and the other differences, even if they were constant, would not be of much significance (see FIG. 2, M, N).

The characteristics of *P. elongatum*, according to Stephani, are the following: the monoicous (paroicous) inflorescence, the very minute pores with only two or three cells around the opening, the trigones in the epidermal cells, the semilunate scales abruptly contracted into one or, rarely, two long, narrowly lanceolate and attenuate appendages, and the shortly emarginate carpocephala bearded below by lanceolate or filiform scales. A study of the type-specimen, however, shows that the pores are almost invariably surrounded by four cells (FIG. 1, H), and although the appendages for the most part agree with the description (FIG. 3, R), some of them are subulate rather than lanceolate, the contraction is more gradual than is implied, and even the narrowest appendages are occasionally duplicated in European material of *P. rupestre*. The other characters, even if constant, would scarcely be differential.

In proposing *Aytonia Evansii* as a new species Miss Haynes compared it with *P. elongatum* and naturally laid a good deal of emphasis on Stephani's description. She points out differences between the two species in size, in the structure of the epidermal pores, and in the form of the ventral scales. She separates her species because the pores are bounded by four or five cells instead of by two or three, and because the scales taper gradually instead of abruptly into the appendages. It has just been shown that the characters upon which she relied are subject to considerable variation in *P. elongatum* and that this species cannot be kept apart from *P. rupestre*. It therefore becomes necessary to reduce *Aytonia Evansii* to a synonym of the same species. At the same time it is a pleasure to recommend the careful and accurate description and figures in Miss Haynes's paper to students of the Hepaticae.

In *P. mexicanum* the original authors apparently had only slight confidence. They say that it is closely allied to *P. rupestre* but that it differs in the more crispate margin of the thallus, in the fact that it is wholly convolute when dry, and in its less conspicuous median canal when moist. They likewise quote a specimen collected by Ecklon and Pappe at the Cape of Good Hope, and although they doubtfully refer this specimen to *P. rupestre*, Lindenberg expresses the opinion that it may be *P. mexicanum*. Stephani adds no differential characters of importance, stating merely that the epidermal cells are surrounded by five or six cells with strongly thickened radial walls, that the epidermal cells have trigones, that the ventral scales have a single appendage, narrowly lanceolate and long-attenuate, and that the carpocephalum is excised at the apex with obtuse, recurved-connivent horns. A portion of the type specimen from the Gottsche herbarium showed most of these characters, although some of the epidermal pores were bounded by only four cells (FIG. 1, E).. The specimen showed nothing, however, to justify the maintenance of *P. mexicanum* as a valid species.

Of *P. lanigerum* authentic material was distributed in Spruce's Hepaticae Spruceanae. In the original description the ventral scales were said to be obliquely triangular and acuminate and the elaters to have four spirals. Stephani adds an account of the epidermal cells, which are said to have trigones, and of the pores, which are said to be surrounded by five cells. He states further that the single appendage of the scales is as long as the basal part, lanceolate in form, and acute, and that the elaters have from two to four spirals. It will be seen at once that there is nothing in either description which would not apply to the variable *P. rupestre*, and Spruce's specimens amply support this position.

In addition to the four species just discussed there are several others recognized by Stephani which are evidently very closely related to *P. rupestre*. Among these are the following: *P. dschallanum*, *P. tenue*, *P. algericum*, *P. nepalense*, *P. chlorocarpum*, *P. validum*, *P. caerulescens*, *P. brasiliense*, *P. peruvianum*, and *P. subplanum*. It is probable that some of these will prove to be synonymous with *P. rupestre*, but unfortunately authentic material has not been available for study. A possible exception may be made in the case of *P. tenue*, which Stephani quotes from three South African regions: the Transvaal, *MacLea*, *Wilms;*

Usambara, *Holst;* and Angola, *Welwitsch.* In the Underwood herbarium there is a specimen from A. Rehmann's Hepaticae austro-africanae, No. 32, collected by MacLea at Müller's Farm in the Transvaal and labeled "*Plagiochasma muricata* Steph." This species was never published but the specimen probably represents *P. tenue,* because no other species of MacLea's Transvaal collection is quoted. Since MacLea's specimen is cited first by Stephani it is even probable that the plant in the Underwood herbarium is part of the type material. The distinguishing characters of *P. tenue* are said to be the following: the dioicous inflorescence (androecia unknown), the very minute epidermal pores surrounded by four cells, the triangular ventral scales bifid two-thirds with parallel, contiguous, narrowly triangular divisions (the latter of course being really the appendages), and the strongly convex carpocephala. MacLea's specimen shows most of these characters except that the carpocephala are distinctly concave. The other characters, moreover, are subject to variation, the pores being sometimes surrounded by five cells and the ventral scales sometimes having a single appendage and sometimes two more or less divergent appendages. In other words the specimen agrees in all essential respects with *P. rupestre.* Whether the other specimens quoted by Stephani represent *P. rupestre* cannot of course be decided, but the probability is that they do.

If *P. rupestre* is accepted in the broad sense of the present paper its geographical distribution becomes very extensive. It is not, however, unique in this respect among the Marchantiaceae. Both *Targionia hypophylla* and *Reboulia hemisphaerica* have a similar and even wider range. Probably if *P. rupestre* extended as far north in Europe as these other two species, it would long ago have been thoroughly known to European writers, and the confusion regarding its synonymy would already have been dispelled.

2. PLAGIOCHASMA CRENULATUM Gottsche

Plagiochasma crenulatum Gottsche, Mex. Leverm. 266. 1863.
Aytonia crenulata Underw. Bot. Gaz. **20**: 66. 1895.

Thallus pale green above but not glaucous, with a narrow purple border, plane or broadly canaliculate, strap-shaped, sparingly forking, sometimes with adventive branches, rarely (if ever) innovating at the apex, margins undulate-crenate, more or less crispate, mostly 1–3 cm. long and 5–10 mm. broad, thickness of thallus about one sixth the width; epidermis composed of thin-walled cells with distinct trigones and a thin smooth cuticle, the cells about 30 μ in diameter; pores slightly elevated, rather small, surrounded by about six (four to seven) radiating series of cells with two or three cells in each series, radial walls slightly thickened; aeriferous layer about three fourths the thickness of the thallus in the median portion, fairly compact with the air spaces about as wide as the green cells or even narrower close to the epidermis; ventral scales lunulate or ovate, purple, slightly overlapping, irregularly sinuous-dentate along the margin with contorted cells, bearing evanescent slime-papillae, cells containing oil-bodies few and scattered, the scales abruptly contracted into one or (more rarely) two large, broadly ovate appendages, short-apiculate or abruptly acute at the apex, irregularly sinuate-dentate along the margin or bearing one or several sharp teeth or even one or two sharp basal lobes: inflorescence monoicous (autoicous): ♂ inflorescence borne on a short ventral branch: ♀ receptacles borne singly or in tandem pairs; peduncle mostly 1–1.5 cm. long; carpocephalum concave at the apex, or obtusely indented, and two- or three-lobed with apiculate lobes, maturing two or three sporophytes; scales of carpocephalum lanceolate to narrowly ovate, irregularly sinuate on the margin or with an occasional tooth: spores about 80 μ in diameter, yellowish brown, minutely verruculose, regularly reticulate, spherical face usually with eighteen to twenty meshes (ten to twelve marginal), plane faces with about seven (five to eight) meshes, those near apex of pyramid less distinct; elaters gradually attenuate, mostly 270–325 μ long and 12 μ wide in maximum diameter, spirals usually three, often coalescing along a longitudinal line. [FIG. 5.]

The following specimens have been examined:

CHIAPAS: San Cristobal, altitude 2,100 m., November, 1907, *G. Münch 5607* (distributed by Levier).

SONORA: Huchuerache, December, 1890, *C. V. Hartman 307* (Lumholtz Expedition).

VERA CRUZ: Orizaba, *F. Müller* (type); February, 1885, *W. G. Farlow;* January, 1892, *J. G. Smith;* December, 1900, *Conzatti & Gonzales;* November, 1908, *Barnes & Land 685;* on wet ground, Cordova, February, 1885, *W. G. Farlow;* on wall along roadside, Cordova, February, 1907, *Miss L. MacIntyre;* along sides of Metlac Gorge, October, 1908, *Barnes & Land 640, 659.*

Gottsche likewise reports the species from Chinantla, PUEBLA, *F. Liebmann.* No other localities are at present known.

Stephani's treatment of this large and distinct species is difficult to understand. He states that the thallus always innovates at the apex, thus implying that dichotomy never occurs, and he adds among other details that the epidermal pores are large and surrounded by eight or nine radiating series of cells with four cells in each series, that the appendages of the ventral scales are ovate-oblong or broadly linear with shortly acuminate apices, and that the apex of the carpocephalum is plano-convex. It would almost seem as if he had not seen the true *P. crenulatum* at all but had drawn his description from some other species. Gottsche's original account is much more accurate, and Leitgeb (**16**, p. 64, *pl. 1, f. 6*) has given an excellent description, with a figure, of the epidermal pores. He calls attention to the fact that the concentric rings of cells surrounding the pore appear as if partially shoved under one another. The pore-opening thus acquires the form of a canal, although the cells all belong to the same epidermal cell-layer. In the material studied by the writer the pores are surrounded by from four to seven radiating series of cells, six being the usual number (FIG. 5, A), and each series is composed of two or three cells. The radial walls are thickened but not very strikingly so. The circular ridge immediately surrounding the opening is distinct in *P. crenulatum* and in all the following species.

The ventral scales develop large and characteristic appendages, usually singly but occasionally in pairs (FIG. 5, C, D). The scales themselves, as in the other members of the genus, are lunulate or ovate in form and overlap slightly. Their cells diminish in size toward the margin and become exceedingly irregular in form and in the direction of their long axes. Some of the marginal cells project and bear vestiges of slime papillae. The appendages are strongly contracted at their junction with the scales and vary considerably in size. Their form, in general, is broadly ovate to orbicular and they narrow abruptly into an apiculate or shortly acute apex, which is tipped with a single cell or with a row of two or three cells. The cell-structure is very similar to that in the scale itself and the border, composed of irregular and contorted cells, is very different from what is found in the narrower scale-appendages of *P. rupestre*, where the cell-structure of the appendages is practically uniform throughout.

A species closely allied to *P. crenulatum* is the East Indian *P. appendiculatum* Lehm. & Lindenb., one of the two species upon which the genus *Plagiochasma* was based. This interesting plant is known to the writer from a series of specimens, including a part of Wallich's original collection in the Mitten herbarium. It is characterized, as Stephani notes, by the large appendages of the ventral scales, cordate or broadly ovate in form, entire, obtuse, and strongly contracted at the base. This description brings out their peculiarities clearly. It may be added that the cell-structure of the appendages is fairly uniform except for a very narrow border, where the cells are somewhat irregular and contorted.

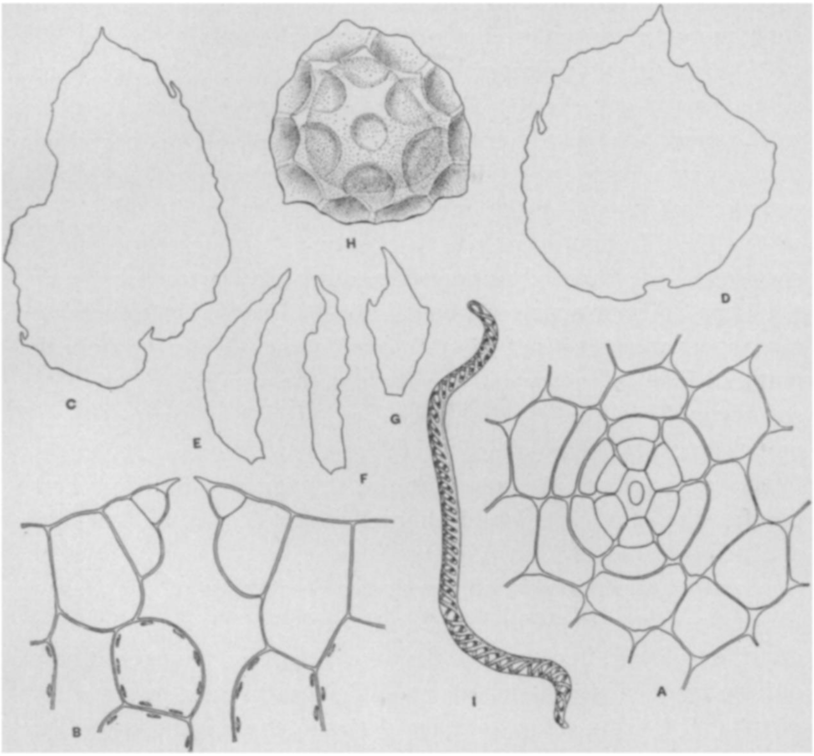

FIG. 5. PLAGIOCHASMA CRENULATUM Gottsche

A. Epidermal pore, surface view, × 300. B. Epidermal pore, cross section, × 300. C, D. Appendages of ventral scales, × 40. E–G. Scales from a carpocephalum, × 40. H. Spore, spherical face, × 225. I. Elater, × 225. The figures were all drawn from specimens collected by Barnes & Land at Orizaba (*685*).

The epidermal cells and pores are much the same as in *P. crenulatum*, although the number of radiating series of cells around a pore is sometimes as high as eight. The spores are distinctly smaller measuring 50–70 μ in diameter (51 μ according to Stephani), but they are reticulate in much the same way, and the elaters usually show more or less coalescence of their spiral bands.

The specimens collected by Hartman in the state of Sonora come particularly close to *P. appendiculatum*, and their reference to *P. crenulatum* must be considered provisional. The appendages of the ventral scales are distinctly orbicular in most cases with rounded apices and entire margins, so that they simulate those of the East Indian species very closely. If it were not for the occasional presence of appendages distinctly narrowed toward the apex or even acute it would be quite justifiable to consider the Sonora plant distinct from *P. crenulatum*. Unfortunately the material is both scanty and sterile, and the appendages are often so thoroughly bleached that their true structure cannot be well made out. It is possible, therefore, that more complete or fertile material would show that the striking peculiarities of the plants were of an accidental character, and for this reason they are included under *P. crenulatum*.

Another specimen which requires a few words of comment is the one collected by Münch at San Cristobal. This specimen was distributed by E. Levier in his Bryotheca under a manuscript name of Stephani. The writer finds no sufficient grounds, however, for separating it from *P. crenulatum* although the appendages of the ventral scales are somewhat smaller and narrower than in typical forms of the species and taper more gradually toward the apex. Combined with this slight difference the epidermal pores exhibit thicker radial walls than is usual and tend to show more than six radiating series of cells around the opening. In other respects the specimen is like *P. crenulatum*.

3. **Plagiochasma jamaicense** (Haynes) comb. nov.

Aytonia jamaicensis Haynes, Bull. Torrey Club 34: 58. *pl. 6.* 1907.

Thallus pale green above but not glaucous, with a reddish purple border, plane or broadly canaliculate, strap-shaped, sometimes with adventive branches, sometimes innovating at the apex, rarely (if ever) dichotomous, margins crenulate, more or less crispate, mostly about 1 cm. long and 5–7 mm. wide, thickness of thallus about one eighth the width; epidermis composed of thin-walled cells with small but distinct trigones and a smooth cuticle, the cells about 30 μ in diameter; pores slightly elevated, rather large, surrounded by about eight (five to ten) radiating series of cells with two to four cells in each series, radial walls slightly thickened; aeriferous layer about three-fourths the thickness of the thallus in the median region, fairly compact, with the air-spaces a little wider than the green cells; ventral scales lunulate to ovate, purple, slightly overlapping, irregularly sinuate along the margin with vestiges of slime papillae, cells containing oil-bodies very few and scattered, the scales abruptly contracted into one or (rarely) two ovate appendages, constricted and plicate at the base, entire or vaguely and irregularly dentate or crenate along the margin, often showing vestiges of slime papillae, gradually narrowed toward the apex into an apiculum usually two to three cells long; inflorescence monoicous: ♂ inflorescence (in the few observed cases) near the apex of a thallus, the ♀ receptacles being borne (usually in a series) on the following joint or apical innovation; peduncle of carpocephalum 1–1.5 cm. long; carpocephalum mostly plano-concave at the apex and bluntly two- to four-lobed, usually maturing two sporophytes; scales of carpocephalum lanceolate to linear-lanceolate, acuminate, entire or sparingly and irregularly dentate: spores 70–85 μ in diameter, yellowish brown, minutely verruculose, reticulate but with the meshes often indistinct, spherical face with about twelve meshes (eight or nine marginal), plane faces with about four meshes; elaters gradually attenuate, mostly 250–375 μ long and 8 μ in maximum diameter, with two or three spirals, sometimes slightly coalescent.

The following specimens have been examined:

JAMAICA: Chestervale, Blue Mountains, altitude 900 m., February, 1903, *L. M. Underwood 1173* (type), *1177* (both mixed with *Reboulia hemisphaerica* [L.] Raddi).

No other localities for the species are known.

The above description is largely compiled from the original paper of Miss Haynes, only a few details having been added. The specimens studied bear a very strong resemblance to the *Reboulia* with which they are growing, the size, general habit, and pigmented margin being almost exactly the same. The color, however, is a trifle redder in the *Plagiochasma* and of course the dorsal position of the carpocephala will at once separate it from the *Reboulia*, where the carpocephala are terminal. The appendages of the ventral scales are likewise very different, those of the *Reboulia* being narrowly linear or lanceolate.

A close relative of *P. jamaicense* is *P. crenulatum*, a somewhat larger and firmer species, the aeriferous layer being a little more compact. In distinguishing the species the best differential characters are drawn from the epidermal pores and ventral scales. Although the pores in the two plants are built up on the same plan, those of *P. jamaicense* tend to be more complex and usually show a greater number of radiating series of cells around the opening with more cells in each series. The ventral scales are much the same in their basal portions except that those of *P. crenulatum* are larger and show a broader border of contorted cells. It is in their appendages that the scales are most distinct. In *P. crenulatum* these are broadly ovate to orbicular, the largest reaching a length of 1–1.4 mm. and a width of about 1 mm.; in *P. jamaicense* they are more narrowly ovate, the largest reaching a length of 0.45 mm. and a width of 0.3 mm. In *P. crenulatum* the apical contraction is usually abrupt, in *P. jamaicense* it is more gradual, and the apex seems to be invariably tipped with a row of two or three cells. Another difference to be noted is in the position of the androecium. In *P. crenulatum* it is borne on a short ventral branch and is apparently never succeeded by female receptacles as is the case in *P. jamaicense*. Unfortunately, as already pointed out, it is unwise to place too much confidence in a difference of this sort. The spores of *P. crenulatum*, finally, are more finely reticulated than in *P. jamaicense*, the spherical face showing eighteen to twenty meshes instead of only twelve.

4. PLAGIOCHASMA WRIGHTII Sulliv.

Plagiochasma Wrightii Sulliv.; A. Gray, Manual, Ed. 2, 688. *pl. 6.* 1856.

Aitonia Wrightii Underw. Bull. Illinois State Lab. Nat. Hist. **2**: 43. 1884.

Thallus pale green and glaucous above, with a narrow purple border, plane or broadly canaliculate, strap-shaped, sometimes forking, sometimes innovating at the apex, sometimes with ventral adventive branches, margins undulate-crenate, more or less crispate, mostly 1.5–2 cm. long and 3–5 mm. broad, thickness of thallus about one fourth the width; epidermis composed of thin-walled cells with distinct trigones often having bulging sides and a thin cuticle with a waxy covering, the cells averaging about 22 μ in diameter; pores slightly elevated, rather small, surrounded by about six (five to eight) radiating series of cells with two or three cells in each series, radial walls distinctly (and sometimes strongly) thickened; aeriferous layer about three fourths the thickness of the thallus, of a rather loose structure, the air spaces about twice as wide as the green cells; ventral scales lunulate, purple, slightly overlapping, irregularly sinuous-dentate along the margin with somewhat contorted cells, bearing evanescent slime-papillae, cells containing oil bodies few and scattered, the scales abruptly contracted into one or two ovate-lanceolate appendages, obtuse to acute at the apex, entire, more or less constricted and plicate at the base: inflorescence monoicous (autoicous): ♂ inflorescence borne behind the ♀ receptacle or on a short ventral branch: ♀ receptacles borne singly or in a median row of two or three; peduncle mostly 1.5–2 mm. long (3–4 mm. long, according to Stephani); carpocephalum narrowly concave at the apex, two- or three-lobed with apiculate lobes, maturing two or three sporophytes; scales of carpocephalum linear-lanceolate, acuminate, entire; spores brownish yellow, 75–85 μ in diameter, minutely rugulose, regularly reticulate, spherical face usually with twelve or thirteen meshes, plane faces each with four meshes, reticulum often incomplete; elaters gradually attenuate, mostly 225–250 μ in length and 7–9 μ in maximum diameter, spirals two or three, often somewhat coalescent. [FIG. 6.]

The following specimens have been examined:

TEXAS: under overhanging rocks along steams, San Marco, 1848, *C. Wright 9* (type).

ARIZONA: Nogales, February, 1902, *D. T. MacDougal.*

COAHUILA: San Lorenzo Canyon, about 3.5 km. southeast of Saltillo, September, 1904, *E. Palmer 423.*

DURANGO: near the city of Durango, 1896, *E. Palmer 862.*

VERA CRUZ: Cordova, without date, *C. Sallé;* Orizaba, February, 1885, *W. G. Farlow 17* (in Farlow herbarium).

No other localities have been reported.

In studying the present species the writer has had the privilege of examining a portion of the type material. Although carpocephala and sporophytes are present, the spores and elaters are poorly or abnormally developed so that it is impossible to gain from them an accurate idea of the typical structure of these organs.

This is fortunately supplied by the specimens collected by Sallé at Cordova.* The specimens from Arizona and the other Mexican specimens listed above lack carpocephala but show clearly the vegetative characters of the species.

Sullivant's original account, which is reproduced with but slight alterations by Underwood, describes the more striking characters of the plant but does not call attention to the structure of the epidermis and of the ventral scales. These deficiencies are partly supplied by Stephani, who states that the epidermal pores are slightly convex and surrounded by two to three concentric series of cells with six cells in each series and that the appendages of the scales are constricted at the base, ovate, acute, and entire. In her discussion of *Aytonia jamaicensis*, Miss Haynes notes that the concentric series of cells around the pores of *P. Wrightii* are composed of from five to eight cells each, instead of being uniformly composed of six cells, as Stephani's description states.

The epidermal pores in *P. Wrightii* agree in all essential respects with those of *P. crenulatum*, except that the radial walls tend to be more distinctly thickened. The epidermis is further distinguished by its somewhat smaller cells and better developed trigones and by the presence of a waxy cuticular covering, these features being apparently associated with a more xerophytic habitat.

Although Stephani's description implies that the ventral scales bear a single appendage it is not unusual to have two such appendages present. They are characterized by their ovate-lanceolate form and acute or obtuse apices, the margins being usually entire and the cell structure fairly uniform. The appendages are somewhat constricted at the base, but the constriction often appears more marked than it really is on account of the folds in the basal portion. The marginal cells of the basal portion (FIG. 6, D) are more or less irregular and contorted and show vestiges of slime-papillae.

As pointed out by Miss Haynes, *P. Wrightii* is related to *P. jamaicense*. She finds differences, however, in the epidermal

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* It may be noted that Berkeley in his Introduction to Cryptogamic Botany (p. 443, *f. 93 a–c*), published in 1857, has figured a carpocephalum and a spore from Sallé's material, under the name *P. mexicanum*.

pores, in the ventral scales, in the length of the peduncle, in the scales of the carpocephalum, and in the spores. Those drawn from the length of the peduncle, from the scales of the carpocephalum and from the spores are perhaps a little untrustworthy and difficult to apply, but the others will serve to distinguish the two species. In *P. Wrightii* the pores are much the same as in *P. crenulatum*, although perhaps a little less elevated; the opening is usually surrounded by six radiating series of cells with two or three cells in each series. In *P. jamaicense* there is a tendency at least toward a greater complexity, many of the pores showing eight radiating series of cells with three or four cells in each series. Of course here, as in so many other cases, it is unsafe to base conclusions on the study of only a few pores, because those of *P. Wrightii* sometimes show as many as eight radiating rows while those of *P. jamaicense* may show as few as six or even five. In most cases the radial wall-thickenings and the trigones are better developed in *P. Wrightii* than in *P. jamaicense*. According to Miss Haynes the appendages in *P. Wrightii* are less constricted and narrower than in *P. jamaicense* with their margins always entire. A study of a considerable amount of material shows that these differences are usually, but not always, present; there are rare cases, for example, where the appendages in *P. Wrightii* are broad enough to be called ovate, where the basal constriction is marked, and

FIG. 6. PLAGIOCHASMA WRIGHTII Sulliv.

A. Epidermal pore, surface view, × 300. B. Ventral scale with two appendages, × 40. C. Appendage from another ventral scale, × 40. D. Cells from the margin of a ventral scale, basal portion, × 225. The figures were all drawn from the specimens collected in the state of Coahuila, *E. Palmer 423*.

where the margin is vaguely denticulate. These broad appendages, however, seem to be always associated with narrower appendages of the usual type and the apices show a much greater degree of variation than in *P. jamaicense*, being sometimes acute and sometimes obtuse.

Although *P. Wrightii* is doubtless a close relative of *P. crenulatum* the two species differ strikingly in appearance. *P. crenulatum* is not only a larger plant but it looks much firmer and more compact owing to the smaller intercellular spaces in the aeriferous layer. It also lacks the waxy covering on the cuticle, which is sometimes conspicuous in *P. Wrightii* and gives the thallus a glaucous aspect. The margin is about as crenulate in *P. Wrightii* as in *P. crenulatum* but the whole marginal region is thinner and more markedly crispate. With respect to branching, *P. crenulatum* rarely, if ever, develops a jointed thallus, while such a condition is usual in *P. Wrightii*. This difference, however, as already emphasized, is one which must be used with caution.

5. **Plagiochasma Landii** sp. nov.

Thallus pale green above but not glaucous, with a narrow purple border, plane or broadly canaliculate, strap-shaped, rarely forking, usually innovating at the apex or with ventral branches. margins undulate, slightly crispate, 1 cm. or less in length, 4–7 mm. in width, thickness of thallus about one sixth the width; epidermis composed of thin-walled cells with small but distinct trigones and a thin smooth cuticle, the cells averaging about 28 μ in diameter; pores slightly elevated, rather small, surrounded by five to seven radiating series of cells with two or three cells in each series, radial walls slightly thickened; aeriferous layer about three fourths the thickness of the thallus in the middle, fairly compact with the air spaces about as wide as the green cells or a little wider, tending to extend at right angles to the epidermis; ventral scales broadly lunulate, purple, entire, cells along the margin smaller, more or less elongated parallel with the margin and with scattered evanescent papillae, cells containing oil-bodies few and scattered, the scales gradually narrowed into a single subulate, acuminate appendage, varying greatly in length, entire or rarely with a sharp tooth, scales sometimes with two such appendages: inflorescence monoicous (paroicous): ♀ receptacles usually borne singly, peduncles very short, usually about 1 mm. long, scales of the carpocephalum lanceolate, acuminate, somewhat contracted at the base, variable in size, the largest about 1.2 × 0.3 mm., about ten cells wide, entire or sometimes with one or two short and irregular teeth, oil-containing cells few and scattered; carpocephalum concave at the apex, usually with two short-apiculate and sometimes connivent lobes and maturing two sporophytes: spores yellowish brown, mostly 70–80 μ in diameter, minutely verruculose, regularly areolate, the spherical face mostly with twelve to fifteen meshes (nine to twelve marginal), plane faces each with four (or five) meshes; elaters about 225 μ long and 12 μ in maximum diameter, usually with two distinct spirals, rarely with three. [FIG. 7.]

The following specimens have been examined:

MORELOS: near Cuernavaca, October, 1908, *Barnes & Land 466;* same locality and date, *C. G. Pringle 10669* (distributed in Plant. Mex. as *P. elongatum*). No. 466 may be designated the type.

A remarkable specimen collected by W. G. Farlow at Orizaba, state of Vera Cruz, and preserved in the Underwood Herbarium, should be noted in this connection. It bears the number 17 and is referred to *P. crenulatum* (see Underwood, Bot. Gaz. **20**: 66. 1895). The long and slender appendages of the ventral scales, however, with acuminate apices, would at once exclude it from *P. crenulatum* and indicate an affinity with *P. Landii.* Possibly it should be referred to this species, but the epidermal pores are not quite characteristic, and it is impossible to decide from the material examined whether the slight differences which the pores show come within the range of variation to be expected. Apparently No. 17 was made up of more than one species; as already noted the specimen in the Farlow herbarium preserved under this number is *P. Wrightii.*

In *P. Landii* the group of species to which *P. crenulatum*, *P. jamaicense* and *P. Wrightii* belong has another member, the relationship being perhaps closest to *P. Wrightii.* In size and texture the species approaches *P. crenulatum* but it differs in habit on account of the many apical joints or innovations which it produces. Compared with *P. Wrightii* the thallus is a trifle larger and firmer.

Here again the epidermal pores and the ventral scales yield some of the most trustworthy differential characters. The epidermal pores tend to be somewhat less complex than in the other members of the group, each radiating series bounding the opening being often composed of only two cells. In this respect it of course recedes most widely from *P. jamaicense*. The cells forming the pore show in a marked degree the peculiarity described by Leitgeb in the case of *P. crenulatum*. They appear as if shoved under one another, and this condition is often so marked that the second and third cells in each radiating series lie almost directly under the cell next the opening. The cells in each series are separated by very thin walls, and the lines of junction between these walls and the cuticle are more or less convex when seen from above, thus giving the pore a somewhat distinctive, flower-like appearance.

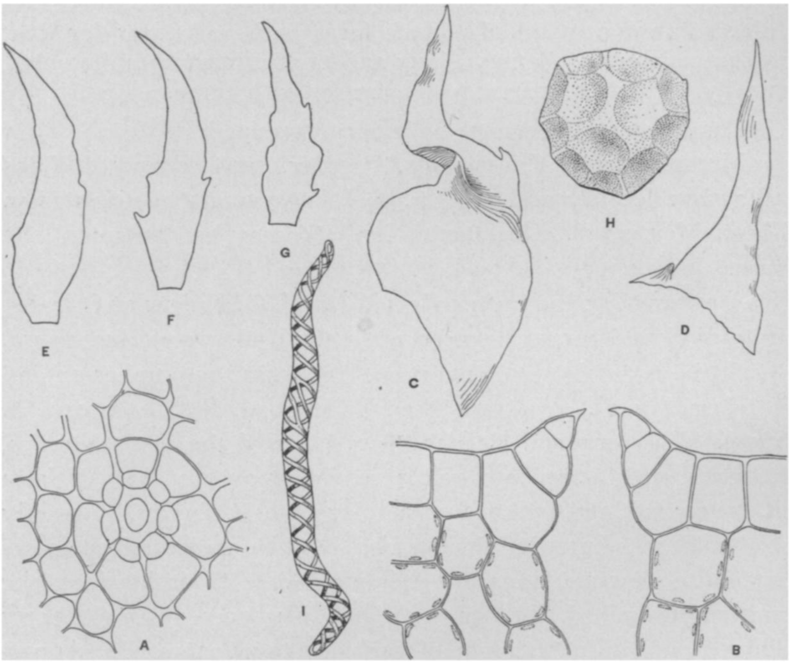

Fig. 7. Plagiochasma Landii Evans

A. Epidermal pore, surface view, × 300. B. Epidermal pore, cross-section, × 300. C. Ventral scale with appendage, × 40. D. Appendage of another ventral scale, × 40. E–G. Scales from a carpocephalum, × 40. H. Spore, spherical face, × 225. I. Elater, × 225. The figures were all drawn from the type specimen.

The ventral scales resemble those of *P. rupestre*, although the basal portion shows a very narrow border of contorted cells and often bears vestiges of slime-papillae. The basal portion is unusually deeply pigmented, and the pale scattered cells containing oil-bodies stand in sharp contrast to the others. The appendages of the scales, sometimes borne singly and sometimes in pairs, are narrowly triangular or subulate in outline and gradually taper to acuminate points, although the extreme apex is often tipped with two cells bearing the vestiges of a slime-papilla between them. There is no sharp line of demarcation between the basal portion and the appendages and the latter are not constricted at the base. For the most part the margins are entire but occasionally an indistinct tooth is present. The appendages are very different from the broad and strongly constricted appendages of *P. crenulatum* and *P. jamaicense.* They resemble more closely the narrow appendages exceptionally found in *P. Wrightii.* The latter species, however, is sure to show appendages of the usual type on some or most of the scales.

6. PLAGIOCHASMA INTERMEDIUM Lindenb. & Gottsche

Plagiochasma intermedium Lindenb. & Gottsche; G. L. & N. Syn. Hep. 513. 1846.

Rupinia intermedia Trevis. Mem. R. Ist. Lomb. III. **4**: 437. 1877.

Aytonia intermedia Underw. Bot. Gaz. **20**: 66. 1895.

Thallus pale green above but not glaucous, with a narrow purple border, plane or broadly canaliculate, strap-shaped, occasionally forking but more usually innovating at the apex, sometimes with ventral adventive branches, margins undulate-crenate, 1 cm. or more long, mostly 3–5 mm. wide, thickness of thallus about one seventh the width; epidermis composed of thin-walled cells with small but usually distinct trigones and a thin, smooth cuticle, the cells averaging about 25 μ in diameter; pores distinctly elevated, large, surrounded by about eight (six to ten) radiating series of cells, with two to four cells in each series, radial walls strongly thickened; aeriferous layer about two thirds the thickness of the thallus, of a loose structure, the air spaces often three or four times as wide as the green cells; ventral scales lunulate, purple, sinuous to crenulate along the margin, some of the marginal cells often contorted, cells containing oil-bodies few and scattered, the scales gradually contracted into two appendages, less often into only one, the appendages slightly or not at all constricted at the base, lanceolate to ovate, entire, usually acute and tipped with a single cell, mostly seven to ten cells wide: inflorescence monoicous: ♂ inflorescence borne near the apex, sometimes on a ventral branch: ♀ receptacles usually borne singly near the apex of the thallus, but sometimes in a median series of two or more, the stalk mostly only 1–2 mm. long; carpocephalum concave with apiculate lobes, commonly maturing two or three sporophytes; scales of carpocephalum lanceolate, acute to acuminate, entire, or rarely with a tooth; spores mostly 60–70 μ in diameter, minutely verruculose, sometimes reticulated, sometimes not, the spherical face then showing a periclinal ridge and one or two irregular supplementary ridges, and each plane face a periclinal ridge; elaters 200–250 μ long and 9–12 μ in maximum diameter, tapering gradually to blunt extremities, usually with uniformly thickened walls and a very narrow cell cavity, rarely with rudimentary spiral bands. [FIG. 8.]

The following specimens have been examined:

JALISCO: near Guadalajara, 1889, *C. G. Pringle 700* (see Underwood, Bot. Gaz. **20**: 66. 1895); wet banks and rocks, Barranca de Oblatos, Guadalajara, September, 1908, *Barnes & Land 136;* moist rocks, Barranca Ibarra o Portella, below Experiencia, September, 1908, *Barnes & Land 146;* banks of streams, road to San Domingo Mine and adjacent gullies and hills, Etzatlan, October, 1908, *Barnes & Land 261.*

PUEBLA: banks along Avenida Hidalgo and path to Barranca Tezuitlan, October, 1908, *Barnes & Land 538.*

VERA CRUZ: San Antonio Huatusco, mixed with *Targionia hypophylla* L., 1857, *C. Mohr 146.*

GUATEMALA: Guachipilin, Dept. Santa Rosa, September, 1893, *Heyde & Lux;* Cuajiniquilapa, Dept. Santa Rosa, August, 1894, *Heyde & Lux* (see Underwood, Bot. Gaz. **20**: 66. 1895). Both specimens were distributed by John Donnell Smith under No. 6292.

JAPAN: Ogawa-mura, Tosa, July, 1900, *T. Yoshinaga 6.*

The species has likewise been reported from several other localities in Mexico and Japan and from the province of Shen-si in China. TYPE LOCALITY: Hacienda de Jovo, VERA CRUZ, *F. Liebmann.*

The remarkable elaters of *P. intermedium* with their uniformly thickened walls will usually serve to distinguish the species from its American allies, even if thickening of this type is not absolutely constant. In the case of sterile specimens the epidermal pores and the ventral scales afford differential characters of importance. The pores are much like those of *P. jamaicense* and tend, if anything, to be even more complex, frequently showing nine radiating series of cells around the opening with four cells in each series. The radial walls separating the series are, moreover, strongly thickened. The ventral scales bear considerable resemblance to those of *P. Landii* and *P. Wrightii*. The basal portion shows a vague border of contorted cells, the margin itself being indistinctly sinuous or crenulate with vestiges of slime papillae. The appendages, usually borne in pairs, are lanceolate to ovate and commonly acute. According to Stephani they are strongly constricted at the base, but this condition is apparent rather than actual and seems to be due to the presence of basal folds. When these are not present the appendages show no appearance of constriction.

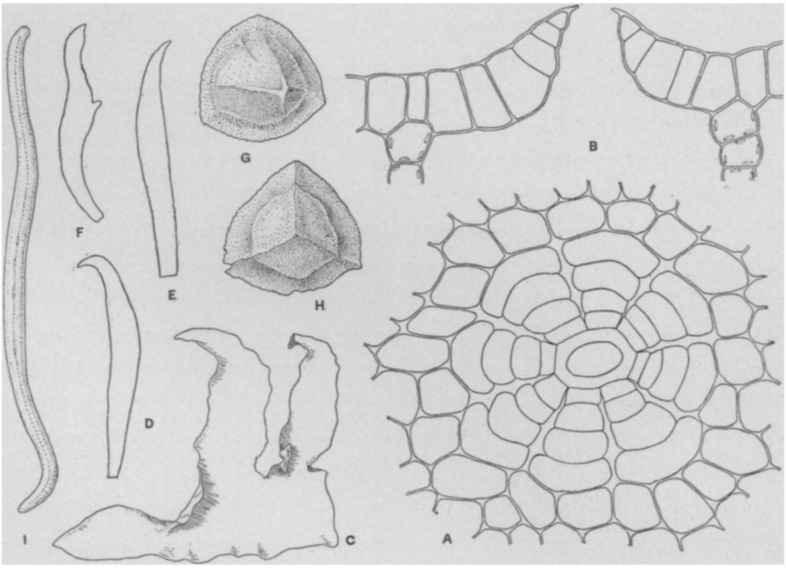

FIG. 8. PLAGIOCHASMA INTERMEDIUM Lindenb. & Gottsche

A. Epidermal pore, surface view, × 225. B. Epidermal pore, cross-section, × 225. C. Ventral scale with two appendages, × 40. D–F. Scales from a carpocephalum, × 40. G. Spore, spherical face, × 225. H. Spore, plane faces, × 225. I. Elater, × 225. The figures were all drawn from the specimens collected by Barnes and Land at Etzatlan (*261*).

Although the appendages are much like those of *P. Landii* and *P. Wrightii* they are distinguished from the first by their blunter apices and from the second, usually at least, by their narrower form and lack of basal constrictions.

In proposing *Aitonia japonica* as a new species Stephani emphasized the solid elaters and spoke of them as a unique feature, apparently overlooking the fact that Gottsche had assigned similar elaters to *P. intermedium* many years earlier. In his Species Hepaticarum, however, Stephani recognizes both *P. japonicum* and *P. intermedium* and ascribes solid elaters to both. A comparison of his descriptions brings out the following differences. In *P. japonicum* the thallus is said to be dichotomous and to innovate from the apex and laterally from the midrib; the epidermal cells to have trigones, and the pores to be surrounded by three or four concentric series of cells with six to eight cells in each series; the appendages of the ventral scales to be ovate-oblong or elliptical; the carpocephalum to be plano-convex with rounded lobes; and the spores to be 50 μ in diameter. In *P. intermedium* the thallus is said to be rarely dichotomous but to innovate from the apex; the epidermal cells to have thick walls but no trigones; the pores to be surrounded by three concentric series with eight cells in each series; the appendages of the ventral scales to be strongly constricted, ovate-oblong, acute, and entire; the carpocephalum to be concave, the lobes showing erect-recurved and connivent horns; and the spores to be 60 μ in diameter.

It will at once be seen that most of these differences are slight or relate to characters which may be expected to be variable. Those drawn from the epidermal cells and from the carpocephala seem at first sight to be more important. Unfortunately they prove to be either inconstant or based on hasty observations. The epidermal cells in *P. intermedium*, for example, have distinct trigones even if they are sometimes small; and the carpocephala in Yoshinaga's specimens of *P. japonicum* are distinctly concave at the apex and show apiculate lobes, agreeing with the usual condition in *P. intermedium*. The writer, in fact, has been able to find no valid characters distinguishing the North American from the Asiatic species and therefore feels compelled to reduce the latter to synonymy, in spite of its wide geographical separation.

The spores reproduced (FIG. 8, G, H) were drawn from the specimens collected at Etzatlan, *261*, and show very few ridges except those along the edges of the tetrahedron. These ridges do not form a reticulum. On the spherical face a continuous wavy ridge is present about half way between the periphery and the center, and from one to three additional ridges extend partly or wholly across the enclosed space. On each plane face a single ridge extends across about half way between the base and apex of the triangles. Unfortunately these spore characters, which at first sight appear so striking, are subject to variation. In the spores of the Guadalajara material, *136*, a regular reticulum is present in most cases, and the two extreme types of spore-structure are connected by a series of intergradations. The Japanese specimens of *P. japonicum* show spores with a diameter of about 70 μ and a well-developed reticulum. In Massalongo's figures, drawn from his variety *chinense*, the reticulum is clearly shown but the number of meshes represented is greater than in the Japanese material. In the Synopsis Hepaticarum a specimen from Nepal is doubtfully included under *P. appendiculatum* as "? *β depauperata*." Gottsche states that this plant is close to *P. intermedium* and implies that the elaters are of the solid type, while Massalongo cites it as a possible synonym of *P. japonicum β chinense*. Unfortunately the lack of specimens has made the study of this form impossible to the writer. It should be remembered, however, that Kashyap occasionally finds solid elaters in *P. appendiculatum*, so that their presence in this doubtful form would not necessarily exclude it from that species. The Synopsis tells us nothing about the epidermis or ventral scales, and Stephani does not mention the plant at all.

The present paper is based on the study of a large series of specimens, including type material of the following previously published species: *P. appendiculatum*, *P. australe*, *P. cordatum*, *P. crenulatum*, *P. elongatum*, *Aytonia Evansii*, *P. eximium*, *P. jamaicense*, *P. lanigerum*, *P. limbatum*, *Reboulia maderensis*, and *P. mexicanum*. For the privilege of studying this rich material the writer is largely indebted to Dr. M. A. Howe, of the New York Botanical Garden, Dr. W. G. Farlow, of Harvard University, Dr. G. Lindau, of the University of Berlin, Professor C. R. Barnes and Dr. W. J. G. Land, of the University of Chicago, and Miss Caroline C. Haynes, of New York City. The collection belonging to the New York Botanical Garden, which includes specimens from the Mitten and Underwood herbaria, has proved particularly helpful. A series of unpublished drawings by Miss Haynes has likewise been of much assistance.

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